THE GENERIC DISTINCTNESS OF *SCHOENOLIRION* and *HASTINGSIA*

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ABSTRACT

Schoenolirion Torrey and *Hastingsia* S. Watson are both representatives of a distinctly North American subtribe of lilies, the Chlorogalinae. The two species groups have been considered to be congeneric in a number of previous publications, but a comparison of morphological traits provides strong support for their generic separation. Comprehensive descriptions of the two genera are provided, along with a synopsis of species included in each.

Historically, the name *Schoenolirion* has been applied to a small group of lilies occurring in several southeastern states and in northern California and southwestern Oregon. Watson (1879) transferred the one western species known at the time (*S. album*) to his new genus *Hastingsia*, but some more recent floras of California and Oregon (Abrams 1923; Jepson 1925, 1936; Munz 1959; Peck 1961; Ferlatte, 1974) continued to use the older generic name.

A comprehensive study of the southeastern species of *Schoenolirion* (Sherman 1969), including a comparison with the western plants (Table 1), provided compelling evidence in support of the generic separation of the two geographically-isolated species groups. Studies of the California/Oregon species by Becking (1986, 1989) have further defined the diversity within *Hastingsia.*

HISTORY OF THE NOMENCLATURE

The nomenclatural history of *Schoenolirion* was reviewed by Sherman (1964) in a proposal (later withdrawn) to conserve *S. album* Durand as the type species of the genus. The name was published originally by Durand (1855) with the description of *S. album,* a plant restricted to northern California and southwestern Oregon. However, *Schoenolirion* was first used by J. Torrey in a manuscript combination, *S. michauxii,* applied to a southeastern species.

Watson (1879) recognized the morphological distinctness of the

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southeastern and western species that previous authors had grouped together as *Schoenolirion.* He considered *Schoenolirion* to be the correct name for the southeastern plants and proposed the new genus *Hastingsia* to include the western species, *H. album,* originally described by Durand.

Schoenolirion was one of the original 405 generic names conserved by the Vienna Congress, 1905, with Rafinesque's *Amblostima* and *Oxytria* listed as nomina rejicienda. Following the adoption of the type method by the Vienna Congress, 1935, *S. album* Durand was proposed as the type species for the genus and was listed as such until Rickett and Stafleu (1959) revised the list of *Nomina Generica Conservanda et Rejicienda.* They proposed *S. michauxii* Torrey as the type species, and its official designation as the type in the Edinburgh Code (1966) fixes the application of the name *Schoenolirion* to the southeastern species.

Relationships

Schoenolirion, Hastingsia and *Chlorogalum* seem to represent a distinct North American group of lilies, a taxonomic alliance first suggested by Watson (1879) when he placed the three genera in the subtribe Clorogalinae. This treatment also was followed by Bentham and Hooker (1883), Krause (1930), and Hutchinson (1959). All three genera may be characterized as being scapose with racemose or paniculate inflorescences and having distinct perianth segments that persist in fruit and anthers that are dorsifixed, versatile and introrsely dehiscent. The fruit in all three genera is a loculicidally dehiscent capsule with two seeds per locule.

Both *Hastingsia* and *Chlorogalum* possess distinct bulbs enclosed by fibrous tunics. *Schoenolirion* is basically bulbous with membranous scales, but is unique in possessing a prominent fleshy rootstock that may best be described as a "vertical rhizome." The rootstock increases in length from year to year (up to 12 cm) because the stem axis persists after the bulb scales or leaf bases are lost. In *S. albiflorum,* the leaf bases are not fleshy and there is some development of a fibrous tunic. In addition to the vertical rootstock, *Schoenolirion* differs from *Hastingsia* in having significantly longer pedicels (6–15 mm), a sessile ovary, an entire or only slightly lobed stigma, and globose seeds with a smooth, glossy coat. In *Hastingsia,* the pedicels are generally much shorter (2–3 mm), the ovary is short-stipitate, the stigma is distinctly 3-lobed, and the seeds are elongated with a rough, reticulated coat. The leaves of *S. croceum* and *S. wrightii* tend to be flat and only slightly keeled, if at all. The leaves of *S. albiflorum* are much more variable, ranging from flattened to almost terete in cross-section and persist as dead foliage at the top of the vertical rootstock. In *Hastingsia,* the leaves are flattened and prom-

inently keeled, and the dead foliage usually is persistent as fibrous tunic around the bulb.

Schoenolirion croceum exhibits a degree of aneuploidy with chromosome numbers $n=12$, $n=15$, $n=16$ usually distinguishing different populations. *S. wrightii* appears to have a constant number of $n=12$, while *S. albiflorum* is a tetraploid with $n=24$. In all cases, the chromosomes of *Schoenolirion* show considerable morphological diversity.

Cave (1970) reported chromosome numbers for *Hastingsia alba* to be $n=26$ or $n=27$ (with query). She also reported $n=15$, $n=17$, $n=18$, and $n=30$ for various species of *Chlorogalum*.

Considering the fact that *Chlorogalum, Hastingsia,* and *Schoenolirion* are all basically bulbous, the subtribe Chlorogalinae should be placed in tribe Scilleae, rather than tribe Asphodeleae. This arrangement would not be without precedent, since Small (1903, 1933) placed *Schoenolirion* (as *Oxytria*) in Scilleae, while Hoover (1940) considered *Chlorogalum* to be a typical member of the Scilleae as defined by Krause.

Dahlgren et al. (1985) included *Schoenolirion, Hastingsia* (as *Schoenolirion*) and *Chlorogalum* in the Family Hyacinthaceae (a taxonomic segregate of the Liliaceae), along with many of the genera traditionally placed in the Scilleae. However, the authors suggested that the three North American genera are peripheral in the Hyacinthaceae and may merit familial rank of their own.

Any discussion of the generic affinities of *Schoenolirion* and *Hastingsia* should include some consideration of *Camassia,* usually placed among the Scillas because of its bulbous habit. The primary distinction between *Camassia* and the three genera of Chlorogalinae is a difference in the number of ovules per locule. *Camassia* has several to many ovules per locule rather than the two that are typical of *Schoenolirion, Hastingsia* and *Chlorogalum.*

Camassia scilloides (Raf.) Cory shares a chromosome number, $n=15$, with some species of *Schoenolirion* and *Chlorogalum,* and it is the only species in any of the four genera (including *Hastingsia*) that exhibits any suggestion of a trans-continental distribution. It occurs sympatrically with *Schoenolirion croceum* in parts of its southeastern range, and the two plants are occasionally found growing together in the same habitat.

Taxonomic Treatment

Schoenolirion Torrey in Durand. J. Acad. Sci. Philadelphia 3:103. 1885. *Nomen conservandum.*—Type: *Schoenolirion michauxii* Torrey—*Amblostima* Raf. Fl. Tellur. 2:26. 1837.—*Oxytria* Raf. Fl. Tellur. 2:26. 1837.

Herbaceous, glabrous perennial with thick, fleshy, vertical rootstock, grass-like leaves, and a simple or branched racemose inflorescence. Vertical rootstock 1–12 cm long, with or without prominent fleshy apical bulb, the rootstock being the persistent stem portion of the bulb that is exposed when the bulb scales wither. Bulb, when present, ovoid or elongated, scales lunate; principal roots from top of vertical rootstock, contractile, persistent 1–2 years. Leaves arising directly from top of rootstock or from bulb, flat or elliptical in transverse section, striate-fibrous. Inflorescence simple or with 1–3 (sometimes more) branches, usually loosely flowered. Bracts short, ¼ to ⅓ of the length of the pedicel. Pedicels slender, jointed at the apex. Flowers yellow or white, often with some red on the abaxial surface, unfertilized ones soon deciduous. Perianth segments 6, distinct, 3–7 nerved, with minute distal tuft of hairs on the adaxial surface, ovate to ovate-oblong, (4.0–)4.5–6.5(–7.5) mm long, (1.5–)2.0–3.5(–4.0) mm wide, withering separately to base, persistent. Stamens 6, of equal length, shorter than the perianth segments, antipetalous ones nectariferous at base; anthers versatile, extrorsely dehiscent, 1–2 mm long. Ovary sessile, globulose, 3-lobed, with axile placentation; ovules 2 per locule, anatropous; style conical, short, about equalling the stamens; stigma minute, entire or very slightly 3-lobed. Capsules globulose, flattened and indented at top, prominently 3-lobed, loculicidally dehiscent, 4.0–6.5 mm broad. Seeds 1–2 per locule, globose, usually flattened on one side, smooth, glossy black, 2–3 mm broad.

Key to *Schoenolirion* Species

a. Leaves without fleshy bases, arising directly from top of vertical rootstock, flat or terete in cross-section, sometimes slightly keeled, withering to persistent fibers; scape robust, much longer than the leaves; inflorescence usually 1–3 branched; perianth segments white or greenish-white. ..... *S. albiflorum*

a′. Leaves arising from a prominent fleshy bulb at top of vertical rootstock, flat to distinctly keeled, bases withering to persistent scales; scape usually simple, with unbranched inflorescence; perianth segments white or yellow.

b. Perianth segments yellow, with green or reddish stripe on abaxial surface, 3–5 nerved; pistils yellow or green; leaves mostly longer than the inflorescence. ..... *S. croceum*

b′. Perianth segments white with green stripe on abaxial surface, mostly 3-nerved; pistils green; leaves mostly shorter than the inflorescence. ..... *S. wrightii*

1. *Schoenolirion albiflorum* (Raf.) Gates, J. Linn. Soc., Bot. 44:167. 1918.—*Amblostima albiflora* Raf., Fl. Tellur. 2:26. 1837.—*Oxytria albiflora* (Raf.) Pollard, Bull. Torrey Bot. Club 24:406. 1897.—Neotype (here designated): Florida, boggy pine barrens near Seville, 7 Jun 1901, *Curtis 6804* (neotype, US!).

Ornithogalum croceum sensu Elliott, Sketch Bot. S. Carolina, 399–

400. 1823. non *Phalangium croceum* Michx., 1803. Rafinesque based the protologue of *Amblostima albiflora* upon Elliott's description of *O. croceum*, plus ". . . a specimen from Elliott himself." Since none of the type material has been found, there is some question concerning the identity of the plant described by Elliott and Rafinesque.

Schoenolirion michauxii Torrey, Bot. Mex. Bound. 220. 1859.—LECTOTYPE (here designated): Buckley, s.n. "East Florida," ex John J. Torrey Herb., with plate of penciled sketches labeled "Phalangium croceum" (lectotype, NY!). Torrey apparently used elements of three species in his description, the Buckley and Chapman specimens mentioned by him being representative of *S. albiflorum*.

Schoenolirion elliottii A. Gray, Amer. Naturalist 10:427. 1876.—LECTOTYPE (here designated): *Chapman s.n.*, "Marshes, Fla." with note: "Don't believe this to be Michaux's plant" (lectotype, GH!).

A tetraploid species differing from *S. croceum* and *S. wrightii* in its much coarser habit, usually branched inflorescence, and lack of fleshy bulb at top of vertical rootstock; occurring in marshy pinelands, cypress bogs, and wet savannahs of southeastern Georgia and throughout most of peninsular Florida; flowering in May in southern part of range, in late May to early June in northern part.

2. *Schoenolirion croceum* (Michaux) Alph. Wood, Am. Bot. & Flor. 344–345. 1870.—*Phalangium croceum* Michaux, Fl. Bor.-Amer. 196. 1803.—*Phalangium croceum* Nutt., Gen. No. Amer. Pl. I: 219–220. 1818.—*Oxytria crocea* Raf., Fl. Tellur. 2:26. 1837.—*Amblostima crocea* Raf., Fl. Tellur. 2:26. 1837.—*Schoenolirion croceum* (Michaux) A. Gray, Amer. Naturalist 10:427. 1876.—TYPE: Georgia, in herbosis humidus sylvarum, *Michaux s.n.* (holotype, P, photo!).

Schoenolirion michauxii Torrey, pro parte, Bot. Mex. Bound. 220. 1859. (Torrey apparently used elements of three species in his description, the Hale collection mentioned by him being representative of *S. croceum.*)

A yellow-flowered species with a prominent bulb at the top of a thick, fleshy rootstock; occurring in organic, acid soil on limestone outcrops in central Tennessee and northern Alabama, sandstone outcrops of the Alabama plateau region, outcrops of Selma chalk in west-central Alabama, granite outcrops of the Georgia Piedmont, moist pinelands and boggy areas of southern Georgia, northern Florida, western Louisiana, and eastern Texas; flowering from mid-March through mid-April in southern and western portion of range, April

through mid-May in northern portion, becoming dormant by late June.

3. *Schoenolirion wrightii* Sherman, Southw. Naturalist 24:123–126, 1979.—TYPE: "wet places on the Colorado of Texas," *Wright, Mexican Boundary Survey 1470* (holotype, NY!).

Schoenolirion michauxii Torrey, pro parte, Bot. Mex. Bound. 220. 1859. (Torrey apparently used elements of three species in his description, the Wright specimen cited by him being representative of *S. wrightii.*)

Schoenolirion texanum A. Gray, Amer. Naturalist 10:426–427. 1876. [This name was based upon *Ornithogalum texanum* Scheele, representative of *Camassia scilloides* (Raf.) Cory, not *Schoenolirion.*]—*Oxytria texana* Pollard, Bull. Torrey Bot. Club 24: 405–406. 1887.

An endangered species very similar to *Schoenolirion croceum,* except for white flowers; highly localized on sandstone outcrops of the Alabama plateau region (Cullman, DeKalb, Cherokee, and Etowah counties) and in wet pinelands and boggy areas of southern Arkansas (Ashley, Bradley, Calhoun, and Drew counties) and eastern Texas (Austin, Brazos, Houston, Walker and Waller counties); flowering from late March to mid-April in Texas and Arkansas, mid-April to early May in Alabama, becoming dormant in mid-June.

Hastingsia (Durand) S. Watson. Proc. Amer. Acad. Arts 14:213–288. 1855.—TYPE: *Hastingsia alba* (Durand) S. Watson.

Schoenolirion Torrey in Durand, pro parte. J. Acad. Nat. Sci. Philadelphia 3:103. 1855.

Herbaceous, glabrous perennial with a fleshy bulb. Bulb ovoid to elongate, densely packed with lunate scales. Leaves grass-like, prominently keeled. Bulb scales and leaf bases shriveling to form fibrous tunica enclosing the bulb. Inflorescence simple to 1–3(–7)-branched with shorter ascending branches, densley flowered. Pedicels 2–3 mm long; perianth segments 6, 3-nerved, white, creamy-white or dark purple, ovate to linear, 5–12 mm long and 1–2 mm wide, tips often triangular, with minute distal glandular hairs on the adaxial surface; tepals withering separately to the base, persistent; stamens 6, with 3 longer and 3 shorter in freshly opened flowers, later being of about equal length. Style with a distinctly 3-parted stigma; ovary globulose, 3-lobed, with axial placentation; ovules 2 per locule, anatropous. Capsule broadly oblong, 6–10 mm long, 5–7.5 mm wide, short-stalked. Seed elongate with shiny black, roughened reticulate coat, usually adaxially flattened.

TABLE 1. SUMMARY OF GENERIC CHARACTER DIFFERENCES BETWEEN *SCHOENOLIRION* AND *HASTINGSIA*.

Schoenolirion	*Hastingsia*
Rootstock a thick, fleshy "vertical rhizome," with or without terminal bulb.	Rootstock ("vertical rhizome") absent.
Bulb, when present, with lunate scales drying to persistent scales around bulb.	Bulb scales densely packed, shriveling to form black, fibrous tunica enclosing the bulb.
Leaves flat or elliptical in cross-section, sometimes slightly keeled, persistent as dead foliage only in *S. albiflorum*.	Leaves prominently keeled or almost terete, often persistent as dead foliage.
Inflorescence (5)12–45(75) flowered raceme.	Inflorescence (15)24–65(110) flowered raceme.
Pedicels of flowers 6–15(30) mm long.	Pedicels of flowers 2–3 mm long.
Perianth segments white or yellow with central green or reddish stripe on abaxial surface.	Perianth segments white, creamy white, or dark purple with central green, yellowish or purplish stripe.
Perianth segments 3–7-nerved 3–5(6) mm long, with distal non-glandular hairs.	Perianth segments 3-nerved, 5–12 mm long, with minute glandular hairs.
Stamens 6, with equal length filaments (1–2 mm long).	Stamens 6, with 3 longer and 3 shorter filaments (4.6–6.6 mm long).
Style with entire or slightly 3-lobed stigma.	Style with distinctly 3-lobed stigma.
Capsule globose, indented at the top, 4–6.5 mm long, 4–6.5 mm wide.	Capsule broadly oblong, 6–10 mm long, 5–7.5 mm wide.
Seeds globose with glossy black, smooth coat.	Seeds elongate with shiny black, rough, reticulate coat.
Chromosome numbers ($n = 12$, $n = 15$, $n = 16$, $n = 24$)—Sherman 1969.	Chromosome numbers ($n = 26$)—Cave 1970.

KEY TO *HASTINGSIA* SPECIES

a. Perianth segments 5–7 mm long and 1–2 mm wide, narrow-lanceolate, white or yellowish tinged with green or pink, usually spreading or sharply reflexed, exposing the stamens.
   b. Scape 28.6–51.4 cm long; bulb small without black fibrous tunic; leaves 21–27 cm long, 2–6 mm wide; perianth lobes 5–6 mm long, sharply reflexed about ⅔ of their length, fully exposing the stamens; raceme mostly unbranched, 3.8–12 cm long, 24–35 flowers per 10 cm of raceme. ..... *H. serpentinicola*
   b′. Scape 40–85 cm long; bulb large, often with black, fibrous tunic; leaves 35–41 cm long, 7–13 mm wide; perianth lobes 5–7.5 mm long, partly closed with tips reflexed outward, exposing only the upper parts of the stamens; racemes mostly 1–4 branched, 14.2–26.9 cm long, 44–51 flowers per 10 cm of raceme. ..... *H. alba*

a′. Perianth segments 8–10 mm long and 2 mm wide, oblong-lanceolate, acuminate, yellowish-white or dark purple-black, fully enclosing the stamens.
   c. Perianth segments dark purple-black with pale green central vein; ovary dark purple; leaves 37.3–44 cm long, 8.4–9.8 mm wide, glaucous green; 30–36 flowers per 10 cm of raceme. ..... *H. atropurpurea*

c'. Perianth segments yellowish-white with a slightly more yellow central vein; ovary dark gray-green; leaves 31.4–38.2 cm long, 5.8–6.7 mm wide, yellowish-green; 25–30 flowers per 10 cm of raceme. ..... *H. bracteosa*

1. *Hastingsia alba* (Durand) S. Watson, Proc. Amer. Acad. Arts 14: 242. 1879.—*Schoenolirion album* Durand, J. Acad. Nat. Sci. Philadelphia 2(3):103. 1855.—TYPE: California, Nevada Co., Deer Creek, *H. Pratten* (lectotype, PH!).

A species of the Klamath Mountains and Cascades–Northern Sierra geological provinces, occurring from southern Oregon (Curry and Josephine counties) through the Northern Coast Range in California (Del Norte, Siskiyou, Trinity, Humboldt, Lake, and Glenn counties) and the northern Cascades and Sierra Nevada Ranges (Shasta, Tehama, Plumas, and Nevada counties); usually found in open, rocky habitats with a good permanent water supply or in bogs or wet meadows, especially at high elevations; flowering May to June, capsules maturing July to August, becoming dormant September to October.

2. *Hastingsia atropurpurea* Becking, Madroño 33(3):175–181. 1986.—TYPE: Oregon, Josephine Co., O'Brien, Woodcock Mt., *Darlingtonia* bog, 4 Jul 1984 (holotype, CAS).

A species restricted to Woodcock Mtn., Tennessee Mtn., and middle and upper parts of the Josephine Creek watershed in Josephine County, OR.; found almost exclusively in permanently wet *Darlingtonia* bogs (sometimes with *H. bracteosa*), occasionally in permanently wet sites on river bars; flowering in May and June, capsules maturing in June and July, becoming dormant at the end of August.

3. *Hastingsia bracteosa* S. Watson, Proc. Amer. Acad. Arts 20:377. 1885. TYPE: Oregon, Curry Co. (=Josephine Co.), Eight Dollar Mt., *Thomas Howell s.n.* (holotype, GH!).

Common but almost totally limited to Eight Dollar Mtn. near Selma, Oregon; occurring on all sides along the base of the mountain, at the mouth of Josephine Creek, the lower parts of Mike's Gulch, Day's Gulch, and Fiddler Gulch; restricted to *Darlingtonia* bogs that remain permanently wet; listed as a candidate endangered species (Federal Register 45:82480–82569, 15 Dec 1980).

4. *Hastingsia serpentinicola* Becking, Madroño 36:208–216. 1989.—TYPE: Oregon, Josephine Co., Cave Junction, Eight Dollar Mt., *Darlingtonia* bog, 28 May, 1985 *R. Becking 850500* (holotype, CAS).

A species occurring almost exclusively on ultramafic or serpentine rock outcrops of the Klamath Mountains and North Coast Range

where it occupies open sites that are moist in the spring and dry out rapidly in early summer. It has recently been segregated from *H. alba* because of its significantly less robust habit, usually unbranched raceme, and sharply reflexed perianth segments.

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